Can N management affect the magnitude of yield loss due to heat waves in wheat and maize?

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Highlights

- We hypothesised that yield penalties produced by heat stress would be modulated by N availability
- We tested the hypothesis in field experiments with heat stress applied as a treatment in maize and wheat crops
- Yield loss due to heat was higher under high than low N availability in both crops
- The increased sensitivity to heat under high N was evident not only in absolute but also as a percentage of the unheated control

Abstract

Deleterious effects of heat on crop yields are well documented and the occurrence of heat stresses will likely be a major constraint to achieving increased yields of major crops. Thus, agronomic and genetic strategies for increased resilience to high temperatures will be necessary. Much of the work done on this area has been focused to identify genetic sources of increased resilience and much less has been done on the crop ecology side. Nitrogen (N) fertilization is within the most common management practices used in cereal production, however, there have been limited efforts to elucidate to what degree the level of soil fertility may affect the magnitude of the high temperature effect on crop yield. The likely interaction may be relevant for designing more appropriate fertilization strategies. We conducted different studies on maize (2009-2012) and wheat (2012-2013), always under field conditions, to determine whether the availability of N may be responsible for the magnitude of the yield penalty imposed by heat stress during reproductive phases (i.e. when heat waves are more likely). We concluded that sensitivity to heat stress increased with increasing N availability and speculated that moderate N stress might produce in the crop plants a sort of acclimation to reduce sensitivity to other stresses. Fertilisation recommendations in the future may need to balance the yielding benefits of high N availability with the detrimental effect of increasing sensitivity to heat stress.

Introduction

Projections to 2050 indicate (i) a still rather relevant world population growth (c. 3 billion more people to be fed), (ii) increases in average wealth (higher consumption *per capita* together with a change in diet, increasing meat consumption; which requires large amounts of cereals due to the low efficiency of grain-to-meat conversion), and (iii) increased needs of biofuel production. All these elements lead to dramatically important increases in demand of cereals in the relatively near future. Projections suggest that a cereal production increase of at least 50% [1, 2, 3], or even more [4, 5, 6] will be needed by 2050.

We have been practising agriculture during the last 10,000 years. In the first 9,950 years since the beginning of agriculture, every time the demand increased there was an expansion of the land used in agriculture [7], driving human migrations; and expansions of human populations have largely been driven by food supply [8]. But land available for crop production has not been increasing much during the last 50 years or so, as most productive land has been into cultivation by then. Further increasing the cropping area would be made at the expense of expanding to fragile ecosystems which would be not sustainable destroying natural ecosystems and jeopardising biodiversity [9, 10] and would also increase the emissions of greenhouse gasses [11, 12]. In fact, due to expected increases in (environmental and economic) sustainability the total amount of cropped land, that has been virtually stabilised during the last half-century, would not increase and may even decline [3, 13].

Therefore, to cope with the expected increased food demand, crop yields must increase substantially within the next 2-3 decades. Paraphrasing Fischer et al. (2011) [14] '*future agricultural growth will be more reliant than ever on raising yields*'. This must be achieved in a context in which crop management should be environmentally more sustainable [15, 16], and when crops will be more frequently exposed to stressful conditions penalising their yields [17]. The Intergovernmental Panel on Climate Change (IPCC) and other studies and analysis conducted over the past decade have concluded that crop production everywhere runs some risk of being negatively affected by climate change that will be continually changing at a relatively rapid rate during this century [17 and references herein]

Among these stresses, the one that is more accurately predicted is that crops will be not only exposed to higher temperatures [18, 19] but also to more frequent events of heat waves [20, 21, 22, 23]. The distinction is relevant, as it seems far simpler to deal with relatively small and constant increase in mean temperatures, producing penalties in yield mainly associated with the acceleration of development and a proportional reduction in accumulated growth, than with heat waves that produce far stronger damages related to impairment of reproductive process, not well studied yet [18, 24]. The more frequent exposure of heat waves is expected regions that currently suffer some exposure to heat waves [25] as well as in those that are relatively cool [26]. All the above applies to field crops in general, including wheat and maize, two crops that play (together with rice) a major role in food security worldwide [27, 28, 29].

Deleterious effects of heat on crop yields are well documented since long time ago [e.g. 30, 31] and the occurrence of heat stresses will likely be a major constraint to achieving increased yields of major crops [32, 33]. This is because high-temperatures produce numerous deleterious consequences on growth and reproduction of crop plants [34, 35, 36, 37]. In terms of components, heat may penalise either the number or the weight of the grains, depending on the timing of occurrence of the heat [e.g. 38, 39. 40, 41, 42].

Agronomic and genetic strategies for increased resilience to high temperatures will be necessary [43]. So far most work has been focused on the genetic strategies, mainly identifying genetic variation [44], and eventually identifying genetic bases for resilience [37, 45]. But breeding solutions, including not only the breeding process itself but also the time normally required for adoption, would take decades [46]. Much less has been done on the crop ecology side. Nitrogen (N) fertilization is within the most common management practices used in cereal production, and frequently crops are fertilized to maximize productivity. However, there have been limited efforts to elucidate to what degree the level of soil fertility may affect the magnitude of the high temperature effect on crop yield. Analysing the likely interaction may be relevant for designing more appropriate fertilization strategies.

Might soil N availability affect the magnitude of the heat penalties on cereal yields?

A possible interaction has been speculated [e.g. 36] suggesting that under higher N availabilities the effect of heat would be less damaging, only based on the assumption that exposure to two simultaneous stresses would be more damaging that to only one. This may well be true when both stresses are imposed simultaneously, but this would not be the case as timing of N fertilisation normally precedes the exposure to heat stress. It may also be possible that crop growth under some level of N limitation might create a sort of acclimation to stress that might then alleviate the effect of heat, if it occurs.

To the best of our knowledge, the explicit proposal, and experimental testing, of the hypothesis that the magnitude of the yield penalties produced by heat stress would be modulated by the availability of N for crop growth has not been made until recently [47, 48]. However, few experiments, mainly under controlled conditions, have been conducted to quantify the effects of high-temperature (most of the times high- and low-temperatures increasing both the maximum and the minimum; i.e. not imposing a heat wave) under high- or low-N availability. As the studies were not explicitly testing the hypothesis the interaction was not reported explicitly but re-analysing the results reported it seemed clear that the magnitude of the penalty increased with in the high- respect to the low-N condition and in most cases the authors did measure grain weight but not yield. In general, the detrimental effect of exposing plants to high temperatures was milder under low- than under high-N availability (Figure 1).

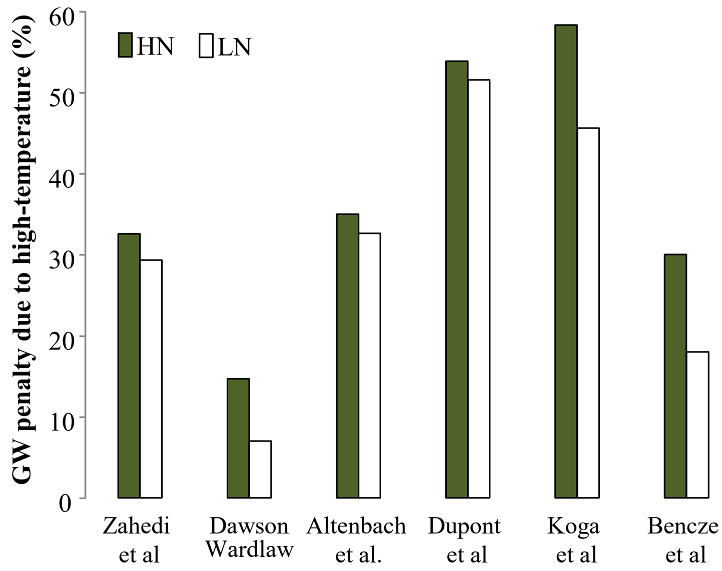


Figure 1. Relative reduction in average grain weight in response to high-temperature stress imposed under either high- or low-N conditions (dark filled and open bars, respectively) from experiments under controlled conditions [49, 50, 51, 52, 53, 54]. Data averaged across cultivars or conditions when more than one was reported and when more than two temperature regimes were included we considered the two extreme cases.

But accepting these results as conclusions that can be applied to crop N management seems inappropriate. Not only because none of these studies were designed to test the interaction but also because they (i) were carried out under controlled conditions that can be hardly extrapolated to real crops (Box 1), and (ii) applied temperature treatments that may be rather unrealistic and in some cases too extreme to represent true changes expected from climatic change.

There was a single case in which heat treatments were imposed in barley grown under field conditions increasing the maximum though not the minimum temperatures from 10 to 20 days after flowering in fertilised and unfertilised plots [55]. They found that grain weight was reduced by the stress, though the magnitude of penalty was dependent on the nitrogen fertilisation (heat treatment reduced grain weight from 44.2 to 37.1 mg grain^{-1} in unfertilised plots and from 45.1 to 34.9 mg grain^{-1} in plots that were fertilised (see Table 1 for untrimmed spikes in [55]). However, results from this study could not be straightforwardly extrapolated to crops actually suffering a heat wave because only the spikes were heated, through enclosing all spikes in 0.5 m of a central row into transparent acrylic boxes with open bases. Therefore, any eventual effect of heat x N on yield through affecting leaf senescence or carbohydrate remobilisation would have been overlooked. There is another field study with wheat but that cannot be used for testing the hypothesis as temperature was increased during both day and night and over the whole growing season [56]. By increasing night temperatures during a severe winter the "high-temperature" was actually a stress-alleviator improving yields though reducing winter damages produced by intense frosts.

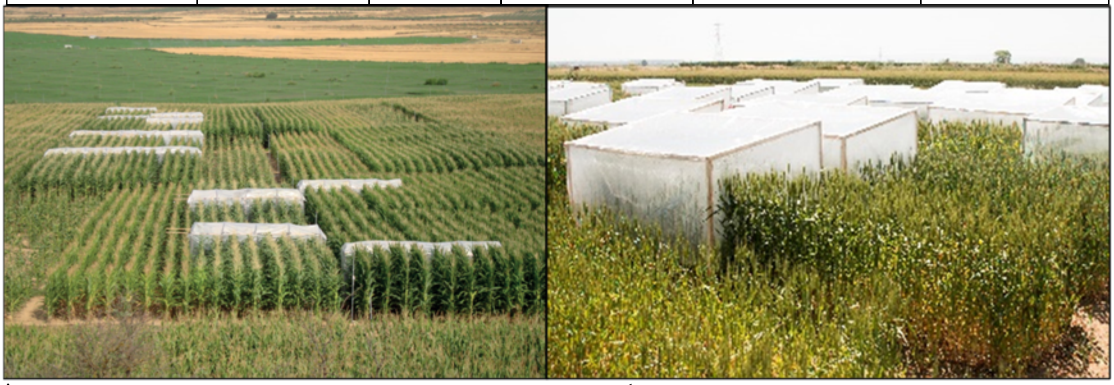
Testing the hypothesis under field conditions

We conducted field studies, in actual farmers' fields on maize [47] and wheat [48], to determine whether the availability of N may be responsible for the magnitude of the yield penalty imposed by heat stress during reproductive phases (i.e. when heat waves are more likely). In each of the experiments, we exposed the crop to the factorial combination of contrasting temperature treatments and at least two contrasting N fertilization regimes (low and high soil N availabilities) (Table 1). For testing the effects of heat stress with minimum bias (see Box 1), we imposed the treatments in the field and within the same experimental design. For that purpose, we enclosed the canopy area designated for the treatments with transparent polyethylene film mounted on wood structures (see illustrations in Table 1), leaving the bottom part of the four sides of each structure open, in order to facilitate gas exchange. Temperature was monitored inside and outside the structures at the height of the spikes in wheat and of both the panicles and the ears in maize. These structures increased the daily maximum temperature by c. 5ºC while left the minimum temperatures virtually unaltered (see details in [47, 48]. Importantly, the high-temperature treatments imposed in all experiments are in line with those expected to occur: only slightly higher than the control when considering the average temperature but characterised by a noticeable increase in maximum temperatures during several days (heat waves).

Table 1. Description of the general characteristics and treatments of the experiments conducted under field conditions considered in the study. At the bottom of the table two pictures illustrate the heat treatments imposed in the field both in maize (left) and wheat (right)

Experiment	**Growing season**	**Crop**	**Genotype**	**Fertilization†**	**Heat stress**
Exp. 1	2009	Maize	Lapopi PR31N28	N0 $N200_{6L}$	Unheated $Heated_{CPGN}$ $Heated_{EGF}$
Exp. 2	2010				
Exp. 3	2011		PR31N28	N0 $N100_{4L†}$ $N100_{S-15†}$ $N200_{4L}$ $N200_{S-15}$ $N200_{4L+S-15}$	
Exp. 4	2012		PR33Y72		
Exp. 5	2012/13	Wheat	Tribat Sensas	$N200_{SE}$	Unheated $Heated_{EGF}$

Exp. 6	2013/14		Nogal Ingenio Rodolfo	N0 $N200_{SE}$	



†fertilisation doses were 0, 100 or 200 KgN ha^{-1} (N0, N100, and N200, respectively), and the timings of application were: 4L and 6L, at the stage of 4 and 6 expanded leaves; S-15, 15 d before silking; SE at the onset of stem elongation. When two stages are noted half of the total dose was applied in each of these stages.

In the unheated controls of all experiments both wheat and maize responded to N fertilisation increasing significantly the crop yield, indicating that in the unfertilised plots both maize and wheat were grown under a moderate N shortage (as yields in unfertilised crops was never negligible: lowest yields were c. 6 and 4.5 Mg ha^{-1} in maize and wheat, respectively). We also found that, as expected, yield was reduced by heat stress. In the case of maize, the heat treatment starting before and finishing after silking (i.e. during the so called 'critical period for grain number determination'; e.g. [57]) produced a massive reduction of yield: averaged across experiments and N conditions a yield loss of c. 70%. Other field experiments with direct imposition of heat stress in the critical period around silking in maize have also shown this sort of collapse of yield [39, 58]. And the reductions were mainly due to direct effects of heat on the capacity of the ovaries to set grains as (i) the magnitude of the yield penalty is enormous compared to relatively minor effects on biomass, and (ii) the collapse is not reverted pollinating the silks with fresh pollen not exposed to heat [40, 47]. The heat treatment imposed during the effective period of grain filing in either maize or wheat produced a highly significant though not massive yield penalty (c. 29% in the experiments with maize and 17% in the experiments with wheat).

All these main (N and temperature) effects on crop yield agree with what can be usually seen in the literature. That is, the general background in which the hypothesis (that the N availability would alter the magnitude of yield reductions produced by heat) represent a common crop condition.

Relevantly, the magnitude of the penalty imposed by the heat was dependent on the N fertilization level (Figure 2). Heat stress induced yield penalties were was much more severe when the treatment was applied in the critical period of grain number determination than in the effective grain filling period, and wheat was apparently less sensitive than maize (though this cannot be concluded rigorously as wheat and maize were not compared in the same experiments). It has been clearly found that well fertilised crops of both wheat and maize were more sensitive to heat than the unfertilised crops. Open symbols representing the unfertilised crops tend to be much closer to the 1:1 ratio than darkly filled symbols representing the highest N-fertilisation condition, whilst the crops fertilised with 100 KgN ha^{-1} were intermediate (Figure 2). It is relevant to notice that in general the higher sensitivity to the heat stress imposed of crops fertilised with 200 KgN ha^{-1} than the unfertilised crops was not only evident in absolute yield losses but also when these losses were determined as a percentage of the yield in the unheated controls within each N-fertilisation condition (Figure 2, right panel).

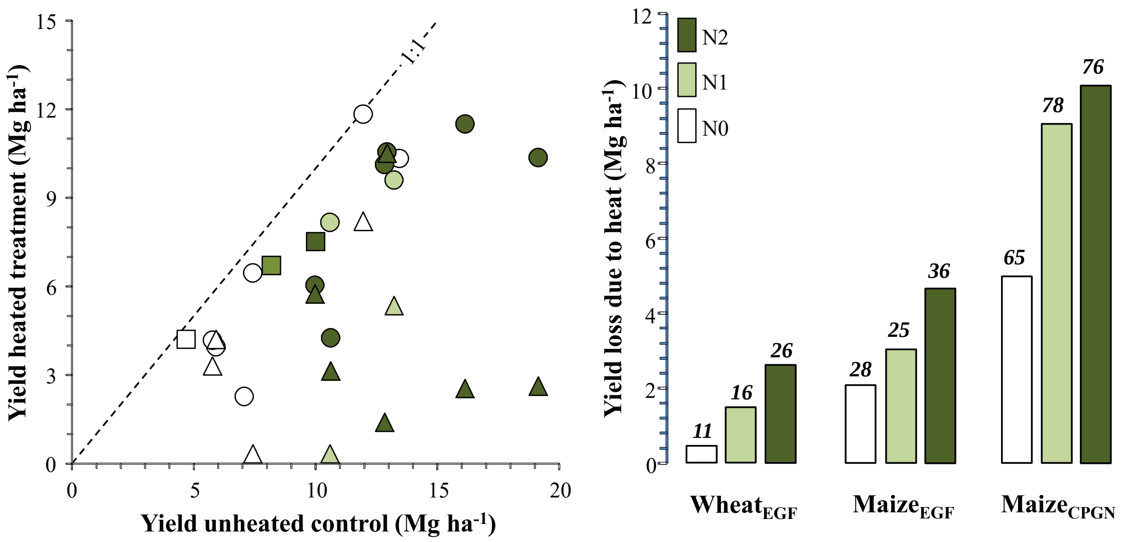


Figure 2. *Left panel*: Yield in the heat stress treatment imposed during the effective grain filling period (EGF) in wheat (squares) and maize (circles) as well as during the critical period for grain number determination (CPGN) around silking in maize (triangles) plotted against the yield in the unheated controls under unfertilised conditions (open symbols) or fertilised with 100 (light symbols) or 200 KgN ha^{-1} (dark symbols). Dashed line stands for Y = X, the 1:1 ratio. *Right panel*: Yield penalty imposed by the heat stress in wheat and maize during their EGFs and in maize during the CPGN. Each bar is the average of

different conditions (experiments, cultivars) in which there was no fertilisation (N0), or plots were fertilised with 100 (N1) or 200 KgN ha^{-1} (N2). Figures on top of each bar stand for the yield penalty as a percentage of the yield in the unheated control.

Regretfully, there seems not to be other field studies of this nature. Therefore, we cannot discuss the consistency of our results with those from other regions/cultivars. Said that, the results we observed were rather consistent across very different experiments and in the case of maize across three different hybrids and 5 different varieties in wheat; as well as with the few cases we found in the literature with experiments carried out under controlled conditions.

As the study of this interaction is in its infancy it would be naïve to offer a strong explanation of its physiological bases. Speculating on possibilities, it may be suggested that plants of a crop growing under some degree of N stress (growth being limited by lack of enough N availability), might experience a sort of 'general acclimation' to stresses and thus become less sensitive to another abiotic stress such as heat. The opposite side of the same coin is that heavily fertilised crops (managed to maximise yield) would become more sensitive to heat stress than if moderately fertilised. Fertilization recommendations that have been mainly based on expected responses of crop yield to improved fertility may need to balance the yielding benefits of high N availability and the detrimental effect such fertilization scheme might have in the event of a heat stress.

Finally, crop simulation models are likely the most commonly used tool for predicting the consequences of climate change on crop productivity. Such models shall develop functions to account for the effects of heat stress [59] and its interaction with N availability, to produce trustworthy predictions.

Simulation models used to scale up the physiological responses of crops to regional or even global levels should be amended to consider the abovementioned different in magnitude of effects from heat waves and from constantly higher temperatures, as well as to take into consideration the level of N nutrition to estimate the expected penalty produced by a heat wave.

Concluding remarks

Based on results from field experiments in which hybrids of maize or cultivars of wheat were subjected to a factorial combination of at least two contrasting N availabilities and two heat stress treatments, we accepted the proposed hypothesis. The magnitude of the yield penalty imposed by heat stress was positively related to the availability of N for crop growth. And this conclusion was not only based on penalties estimated in absolute values: higher yielding crops may naturally allow for larger losses, and yield of the unheated controls were much larger in fertilised than in unfertilised crops. Penalties estimated as a percentage of yield under unheated conditions of the same N treatment strengthened the conclusion that sensitivity to heat stress actually increased with increasing N availability. Therefore, in the context of climate changes that will concur with more frequent episodes of heat stress, N fertilisation recommendations may have to be carefully design to avoid further yield penalities.

Box 1. Discussion on approaches to experimentally assess high temperature effects

The effect of high temperature on crop yield has been quantified with a range of methods. By far, the most common approach has been growing potted individual plants under controlled-environment facilities. This is because in this approach temperature can be changed independently of any other factor to any level as well as at any particular timing that researchers want to test. However, this approach has a major drawback. Plant traits in the "control" as well as responses to high temperature can differ considerably from the same plants should they be in real crops. Therefore, although results are normally clean and easy to interpret they cannot be straightforwardly extrapolated to real crops. There are a number of reasons why the conclusions from this approach are many times irrelevant to understand crop performance, the most relevant ones are that (i) performance of isolated plants very rarely represent that of the same plant when grown in a dense crop canopy [60, 61], (ii) roots confined in small pots do not represent at all what they may explore in the field [62, 63], and (iii) the imposition of treatments are frequently different to what actually experience plants in the field: the daily transition from minimum to maximum and back to minimum temperature is quite gradual in real fields while in most controlled-environment facilities this transition is represented by a square-wave temperature regime (and the daily sudden change in extreme temperatures affect plant performance by itself; [64, 65]). For all these reasons, it is extremely difficult to trustworthily scale up results obtained in experiments under controlled conditions to the real fields where conclusions matter [66, 67].

If conclusions are to be valid for direct extrapolation to real crops, work must be carried out under field conditions with plants grown in normal crops stands (high density). However, the imposition of high temperature under field condition is challenging. Indirect and direct methods have been designed and deployed, as nicely discussed in a series of papers by Sadras´s group in grapewine and chickpea [68]. Indirect methods compare results from different growing seasons, regions or sowing dates. Although practical and inexpensive, results from these indirect approaches are bound to remain inconclusive because temperature effects are necessarily confounded with those from other climatic factors, management practices and soils properties that also change [69, 70]. Furthermore, these field-experimental approaches would only allow for testing the effect of exposure to a constant higher temperature (that corresponding to the location, season, sowing date with higher temperatures) but not to heat waves independently. The unique solution is to impose high-temperature treatments directly in the field. Normally the experimental errors are noticeably higher than under controlled conditions, but the increase in reliability on the validity of conclusions makes the field experiments essential. Alternatives for this include the use of portable polyethylene chambers that can be installed and dismounted at any time creating a sort of "greenhouse" effect in the plots assigned to the high-temperature treatment. One of the difficulties of this method with simple chambers is the high relative humidity inside the chambers and the reduction in incident PAR due to the polyethylene films [47, 48, 71, 72, 73]. However, leaving open part of the "chamber" and using "placebos" in which the control is covered only with the "roof" of the chamber (reducing PAR but unaffecting temperature; e.g. [58]). Open-top chambers [74] and infrared heaters suspended above the canopy [75] are likely the best technological options; but with the drawback that they are expensive and difficult to implement at real farmer´s fields.

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References

1. Reynolds, M., Foulkes, M.J., Slafer, G.A., Berry, P., Parry, M.A.J., Snape, J.W., Angus, W.J.: **Raising yield potential in wheat.** *J. Exp. Bot.* 2009, **60**: 1899-1918.

2. Bruinsma, J. **The resources outlook: by how much do land, water and crop yields need to increase by 2050?** In: Looking ahead in world food and agriculture. Perspectives to 2050. (Conforti P., Ed.). Food and Agriculture Organization of the United Nations; 2011: 233-278.
3. Fischer, R.A., Byerlee, D., Edmeades, G.O. **Crop yields and global food security: will yield increase continue to feed the world?** Australian Centre for International Agricultural Research; 2014: 634
4. Rosegrant, M.W., Ringler, C., Zhu, T.J.: **Water for agriculture: maintaining food security under growing scarcity**. *Ann. Rev. Env. Resour*. 2009, **34**: 205-222.
5. Hall, A.J., Richards, R.A.: **Prognosis for genetic improvement of yield potential and water-limited yield of major grain crops**. *Field Crops Res*. 2013, **143**: 18–33.
6. Ray, D.K., Mueller, N.D. West, P.C., Foley, J.A.: **Yield trends are insufficient to double global crop production by 2050**. *PLoS ONE* 2013, **8**(6): e66428. doi:10.1371/journal.pone.0066428.
7. Brown, L.R. Full Planet, Empty Plates: The New Geopolitics of Food Scarcity. W W Norton & Company, 2012.
8. Foley, S.F., Gronenborn, D., Andreae, M.O., Kadereit, J.W., Esper, J., Scholz, D., Pöschl, U., Jacob, D.E., Schöne, B.R., Schreg, R., Vött, A., et al.: **The Palaeoanthropocene – The beginnings of anthropogenic environmental change**. *Anthropocene* 2013, **3**: 83-88.
9. Cassman, K.G.: **Ecological intensification of cereal production systems: yield potential, soil quality, and precision agriculture**. *Proc. Natl. Acad. Sci. USA* 1999, **96**: 5952-5959.
10. Tilman, D., Cassman, K.G., Matson, P.A., Naylor, R., Polasky, S. **Agricultural sustainability and intensive production practices**. *Nature* 2002, **418**: 671-677.
11. Searchinger, T., Heimlich, R., Houghton, R.A., Dong, F., Elobeid, A., Fabiosa, J., Tokgoz, S., Hayes, D., Yu, T.H.: **Use of U.S. croplands for biofuels increases greenhouse gases through emissions from land-use change**. *Science* 2008, **319**: 1238-1240.
12. van Wart, J., Kersebaum, K.C., Peng, S., Milner, M., Cassman, K.G.: **Estimating crop yield potential at regional to national scales**. *Field Crops Res*. 2013, **143**: 34-43.
13. Albajes, R., Cantero-Martínez, C., Capell, T., Christou, P., Farre, A., Galceran, J., López-Gatius, F., Marin, S., Martín-Belloso, O., Motilva, M.J., et al.: **Building bridges: an integrated strategy for sustainable food production throughout the value chain**. *Mol. Breeding* 2013, **32**: 743-770.
14. Fischer, T.R., Byerlee, D., Edmeades, G.O. Can technology deliver on the yield challenge to 2050? In: Looking ahead in world food and agriculture. Perspectives to 2050. (Conforti P., Ed.). Food and Agriculture Organization of the United Nations, 2011:389-462.
15. Godfray, H.C.J. 2011. Food for thought. Proc. Natl Acad. Sci. USA 108, 19845-19846.
16. Tilman, D., Balzer, C., Hill, J., Befort B.L.: **Global food demand and the sustainable intensification of agriculture**. *Proc. Natl Acad. Sci. USA* 2011, **108**: 20260-20264.
17. McKersie, B.: **Planning for food security in a changing climate**. *J. Exp. Bot*. 2015, **66**: 3435-3450.
18. Lobell, D.B., Bänziger, M., Magorokosho, C., Vivek, B.: **Nonlinear heat effects on African maize as evidenced by historical yield trials**. *Nat. Clim. Change* 2011, **1**: 42–45.
19. Challinor, A.J., Watson, J., Lobell, D.B., Howden, S.M., Smith, D.R., Chhetri, N., 2014. **A meta-analysis of crop yield under climate change and adaptation**. *Nat. Clim. Change* 2014, **27**: 287–291.
20. Meehl, G.A., Tebaldi, C.: **More intense, more frequent, and longer lasting heat waves in the 21st century**. *Science* 2004, **305**: 994-997.
21. Asseng, S., Foster, I., Turner, N.C.: **The impact of temperature variability on wheat yields**. *Global Change Biol*. 2011, **17**: 997–1012.
22. Seneviratne, S.I., Donat, M.G., Mueller, B., Alexander, L.V.: **No pause in the increase of hot temperature extremes**. *Nat. Clim. Change* 2014, **4**: 161-163.
23. Barlow, K.M., Christy, B.P., O'Leary, G.J., Riffkin, P.A., Nuttall, J.G.: **Simulating the impact of extreme heat and frost events on wheat crop production**. **A review**. *Field Crops Res*. 2015, **171**: 109–119.*

24. Sadras, V.O., Vadez, V., Purushothaman, R., Lakea, L., Marrou, H.: **Unscrambling confounded effects of sowing date trials to screen for crop adaptation to high temperature**. *Field Crops Res*. 2015, **177**: 1-8.*
25. Sánchez, E., Gallardo, C., Gaertner, M.A., Arribas, A., Castro, M.: **Future climate extreme events in the Mediterranean simulated by a regional climate model: a first approach**. *Glob. Planet. Change* 2004, **44**: 163–180.
26. Semenov, M.A.: **Development of high-resolution UKCIP02-based climate change scenarios in the UK**. *Agric. Forest Meteorol*. 2007, **144**: 127–138.
27. Reynolds, M., Foulkes, J., Furbank, R., Griffiths, S., King, J., Murchie, E., Parry, M., Slafer, G.A.: **Achieving yield gains in wheat**. *Plant Cell Environ*. 2012, **35**: 1799-1823.
28. Shewry, P.R., Hey, S.J.: **The contribution of wheat to human diet and health**. *Food Energy Secur*. 2015, **4**: 178–202.
29. Shiferaw, B., Prasanna, B.M., Hellin, J., Bänziger, M.: **Crops that feed the world 6. Past successes and future challenges to the role played by maize in global food security**. *Food Sec*. 2011, **3**: 307-327.
30. Wardlaw, L.F., Dawson, I.A., Manibi, P., Fewster, R.: **The tolerance of wheat to high temperature during reproductive growth. I. Survey procedures and general response patterns**. *Aust. J. Agric. Res*. 1989, **40**: 1-13.
31. Wilhelm, E.P., Mullen, R.E., Keeling, P.L., Singletary, G.W.: **Heat stress during grain filling in maize: effects on kernel growth and metabolism**. *Crop Sci*. 1999, **39**: 1733-1741.
32. Hawkins, E.D., Fricker, T.E., Challinor, A.J., Ferro, C.A.T., Ho, C.K., Osborne, T.M.: **Increasing influence of heat stress on French maize yields from the 1960s to the 2030s**. *Global Change Biol*. 2013, **19**: 937-947.
33. Asseng, S., Ewert, F., Martre, P., Rötter, R.P., Lobell, D.B., Cammarano, D., Kimball, B.A., Ottman, M.J., Wall, G.W., White, J.W., Reynolds, M.P., et al.: **Rising temperatures reduce global wheat production**. *Nat. Clim. Change* 2015, **5**: 143-147.*
34. Wahid, A., Gelani, S., Ashraf, M., Foolad, M.R.: **Heat tolerance in plants: an overview**. *Environ. Exp. Bot*. 2007, **61**: 199-223.
35. Barnabás, B., Jäger, K., Fehér, A.: **The effect of drought and heat stress onreproductive processes in cereals**. *Plant Cell Environ*. 2008, **31**: 11–38.
36. Farooq, M., Bramley, H., Palta, J.A., Siddique, K.H.M.: **Heat stress in wheat during reproductive and grain-filling phases**. *Critical Rev. Plant Sci*. 2011, **30**: 491-507.
37. Cossani, C.M., Reynolds, M.P.: **Physiological traits for improving heat tolerance in wheat**. *Plant Physiol*. 2012, **160**: 1710-1718.
38. Ugarte, C., Calderini, D.F., Slafer, G.A.: **Grain weight and grain number responsiveness to pre anthesis temperature in wheat, barley and triticale**. *Field Crops Res*. 2007, **100**: 240–248.
39. Cicchino, M., Rattalino Edreira, J.I., Uribelarrea, M., Otegui, M.E.: **Heat stress in field-grown maize: response of physiological determinants of grain yield**. *Crop Sci*. 2010, **50**: 1438-1448.
40. Rattalino Edreira, J.I., Budakli Carpici, E., Sammarro, D., Otegui, M.E.: **Heat stress effects around flowering on kernel set of temperate and tropical maize hybrids**. *Field Crops Res*. 2011, **123**: 62–73.
41. Rattalino Edreira, J.I., Otegui, M.E.: **Heat stress in temperate and tropical maize hybrids: a novel approach for assessing sources of kernel loss in field conditions**. *Field Crops Res*. 2013, **142**: 58–67.
42. Prasad, P.V.V., Djanaguiraman, M.: **Response of floret fertility and individual grain weight of wheat to high temperature stress: sensitive stages and thresholds for temperature and duration**. *Funct. Plant Biol*. 2014, **41**: 1261–1269.
43. Prasad, P.V.V., Bheemanahalli, R., Jagadish, S.V.K.: **Field crops and the fear of heat stress - opportunities: challenges and future directions**. *Field Crops Res*. 2017, **200**: 114-121.*
44. Devasirvatham, V., Tan, D.K.Y., Trethowan, R.M.: Breeding Strategies for Enhanced Plant Tolerance to Heat Stress. In: Advances in Plant Breeding Strategies: Agronomic, Abiotic and Biotic Stress Traits (Al-Khayri, J.M., Jain, S.M., Johnson, D.V., Eds.). Springer International Publishing, 2016: 447-469.

45. Frey, F.P., Presterl, T., Lecoq, P., Orlik, A., Stich, B.: **First steps to understand heat tolerance of temperate maize at adult stage: identification of QTL across multiple environments with connected segregating populations**. *Theor. Appl. Genet.* 2016, **129**: 945-961.*
46. Hall, A.J., Richards, R.A.: **Prognosis for genetic improvement of yield potential and water-limited yield of major grain crops**. *Field Crops Res*. 2013, **143**: 18–33.
47. Ordoñez, R.A., Savin, R., Cossani, C.M., Slafer, G.A.: **Yield response to heat stress as affected by nitrogen availability in maize**. *Field Crops Res*. 2015, **183**: 184–203.**
48. Elía, M., Slafer, G.A., Savin, R.: **Yield and grain weight responses to post-anthesis increases in maximum temperature under field grown wheat as modified by nitrogen supply**. *Field Crops Res*. 2018, **221**: 228-237.**
49. Zahedi, M., McDonald, G., Jenner, C.F.: **Nitrogen supply to the grain modifies the effects of temperature on starch and protein accumulation during grain filling in wheat**. *Aust. J. Agric. Res*. 2004, **55**: 551–564.
50. Dawson, I.A., Wardlaw, I.F.: **The influence of nutrition on the response of wheat to above-optimal temperature**. *Aust. J. Agric. Res*. 1984, **35**: 129–137.
51. Altenbach, S.B., DuPont, F.M., Kothari, K.M., Chan, R., Johnson, E.L., Lieu, D.: **Temperature, water and fertilizer influence the timing of key events during grain development in a US spring wheat**. *J. Cereal Sci*. 2003, **37**: 9–20.
52. Dupont, F.M., Hurkman, W.J., Vensel, W.H., Tanaka, C., Kothari, K.M., Chung, O.K., Altenbach, S.B.: **Protein accumulation and composition in wheat grains: effects of mineral nutrients and high temperature**. *Eur. J. Agron*. 2006, **25**: 96–107.
53. Koga, S., Böcker, U., Moldestad, A., Tosi, P., Shewry, P.R., Mosleth, E.F., Kjersti Uhlen, A.: **Influence of temperature on the composition and polymerization of gluten proteins during grain filling in spring wheat (Triticum aestivum L.)**. *J. Cereal Sci*. 2015, **65**: 1–8.
54. Bencze, S., Keresztényi, E., Veisz, O.: **Change in heat stress resistance in wheat due to soil nitrogen and atmospheric CO2 levels**. *Cereal Res. Commu*n. 2007, **35**: 229–232.
55. Passarella, V.S., Savin, R., Slafer, G.A.: **Are temperature effects on weight and quality of barley grains modified by resource availability?** *Aust. J. Agric. Res*. 2008, **59**: 510–516.
56. Liu, L., Hu, C., Olesen, J.E., Ju, Z., Yang, P., Zhang, Y.: **Warming and nitrogen fertilization effects on winter wheat yields in northern China varied between four years**. *Field Crops Res*. 2013, **151**: 56–64.
57. Westgate, M.E., Otegui, M.E., Andrade, F.H.: Physiology of the corn plant. In: Corn: Origin, History, Technology, and Production (Smith, C.W., Betran, J., Runge, E.C.A., Eds.), John Wiley and Sons, 2004: 235-271.
58. Rattalino Edreira, J.I., Otegui, M.E.: **Heat stress in temperate and tropical maize hybrids: differences in crop growth, biomass partitioning and reserves use**. *Field Crops Res*. 2012, **130**: 87–98.
59. Gabaldón-Leal, C., Webber, H., Otegui, M.E., Slaferd, G.A., Ordóñez, R.A., Gaiser, T., Lorite, I.J., Ruiz-Ramos, M., Ewert, F.: **Modelling the impact of heat stress on maize yield formation**. *Field Crops Res*. 2016, **198**: 226-237.
60. Pedro, A.' Savin, R., Slafer, G.A.: **Crop Productivity as related to single-plant traits at key phonological stages in Durum wheat**. *Field Crops Res*. 2012, **138**: 42-51.
61. Lake, L., Li, Y., Casal, J.J., Sadras, V.O.: **Negative association between chickpea response to competition and crop yield: phenotypic and genetic analysis**. *Field Crops Res*. 2016, **196**: 409–417.
62. Passioura, J.B.: **Soil conditions and plant growth**. *Plant Cell Environ*. 2002, **25**: 311–318.
63. Passioura, J.B.: **The perils of pot experiments**. *Funct. Plant Biol*. 2006, **33**: 1075–1079.
64. Stone, P. J., and Nicolas, M. E.: **Comparison of sudden heat stress with gradual exposure to high temperature during grain filling in two wheat varieties differing in heat tolerance. I. Grain growth.** *Aust. J. Plant Physiol*. 1995, **22**: 935–44.
65. Savin, R., Stone, P.J., Nicolas, M.E., Wardlaw, I.F: **Grain growth and malting quality of barley 2. Effects of temperature regime before heat stress**. *Aust. J. Agric. Res*. 1997, **48**: 625–34.

66. Passioura, J.B.: **Scaling up: the essence of effective agricultural research**. *Funct. Plant Biol*. 2010, **37**: 585–591.
67. Sadras, V.O., Richards, R.A.: **Improvement of crop yield in dry environments: benchmarks, levels of organisation and the role of nitrogen**. J. *Exp. Bot*. 2014, **65**: 1981–1995.
68. Sadras, V.O., Bubner, R., Moran, M.A.: **A large-scale, open-top system to increase temperature in realistic vineyard conditions**. *Agricultural and Forest Meteorology* 2012, **154**: 187– 194.
69. Sadras, V.O., Soar, C.J.: **Shiraz vines maintain yield in response to a 2–4 ◦C increase in maximum temperature at key phenostages**. *Eur. J. Agron*. 2009, **31**: 250–258.
70. Sadras, V.O., Vadez, V. Purushothaman, R., Lake, L., Marrou, H.: **Unscrambling confounded effects of sowing date trials to screen for crop adaptation to high temperature**. *Field Crops Res*. 2015, **177**: 1–8.*
71. Rawson, H. M., Gifford, R. M., Condon, B.N.: **Temperature gradient chambers for research on global environment change. I. Portable chambers for research on short-stature vegetation**. *Plant Cell Environ*. 1995, **18**: 1048-1054.
72. Savin, R., Stone, P.J., Nicolas, M.E.: **Responses of grain growth and malting quality of barley to short periods of high temperature in field studies using portable chambers**. *Aust. J. Agric. Res*. 1996, **47**: 465–477.
73. Pérez, P., Morcuende, R., Martín del Molino, I., Martínez-Carrasco, R.: **Diurnal changes of Rubisco in response to elevated CO2, temperature and nitrogen in wheat grown under temperature gradient tunnels**. *Environ. Exp. Bot*. 2005, **53**:13-27.
74. Klein, J.A., Harte, J., Zhao, X-Q.: **Dynamic and complex microclimate responses to warming and grazing manipulations**. *Global Chance Biol*. 2005, **11**: 1440-1451.
75. Wan, S., Luo, Y., Wallace, L.L.: **Changes in microclimate induced by experimental warming and clipping in tallgrass prairie**. *Global Chance Biol*. 2002, **8**: 754-768.